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The eco-physiology of the colonial alga *Phaeocystis pouchetii*

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SUMMARY

Field surveys carried out in the spring of 1984 in the eutrophicated coastal zone of the North Sea showed that the spring bloom of phytoplankton is characterized by two major events (chapter 2). In early spring a blooming of diatoms occurs which is followed by a vigorous outburst of the polymorphic alga Phaeocystis pouchetii. The highest cell numbers of Phaeocystis were observed in the near coastal zone with a seaward decreasing number over a transect perpendicular to the coast. This suggests a close relation between the initial nutrient concentration, which decreases also in a seaward direction, and the Phaeocystis biomass. Although the peak of Phaeocystis occurs after that of the diatoms, Phaeocystis is already present in small numbers in early spring and even in winter. During the peak of the bloom the inorganic nitrogen concentration is low, while in most cases inorganic phosphate was depleted. These low phosphate concentrations, and consequently the high N/P ratios, suggest that phytoplankton in the coastal waters of the North Sea is probably phosphate limited (chapter 2).

The present study aimed to investigate some of the eco-physiological properties of Phaeocystis enabling this species success in its natural environment. Close examination of cultures and field samples showed the presence of two major growth forms: single flagellated cells, and immotile cells enclosed in spherical colony matrices. A third form, tiny flagellated cells ("microflagellates") was observed only by the end of the growth period (chapters 2 and 5). It was shown that the transition of one growth form (single cell) into the other (colonies) was affected by the nutrient concentration (chapter 5). Low phosphate levels significantly increased the number of single cells which formed a colony membrane. Subsequently cell division took place within this colony envelope, thereby developing into a colony.

As long as growth conditions were optimal no differences could be found in growth rate or phosphate assimilation rate between either of the two cell types (chapters 5 and 6). In

contrast, at low phosphate levels both cell types differed in their behaviour: colony cells reduced their growth rate as well as their phosphate uptake rate (in short-term experiments). The reduction of the phosphate uptake rate is considered to be the result of diffusion barriers caused by the colony membrane and enclosed mucilage. Nonetheless, supply of the cells with phosphate is still possible because the colony cells use certain properties of the colonial organization, which they are capable to control. These properties are not available to single cells of Phaeocystis. For instance, colony cells maintain the uptake of phosphate in the dark at a high rate, this in contrast to single cells. The colony matrix is thought to function as a phosphate pool. Furthermore, the absorption of phosphate by the whole colony is thought to be positively affected because the surface of the colony exceeds 4 to 10 times the sum of the surfaces of the individual cells.

The view that a Phaeocystis colony can be regarded as a physiological unit is substantiated by the observations on the carbon fluxes (chapters 3 and 4). The high extracellular release of newly fixed carbon, which accompanies photosynthesis of Phaeocystis, appeared to be mainly the excretion of high-molecular-weight-compounds (> 1800 MW) which remained inside the colony membrane. In the subsequent dark period this pool, besides the intracellular reserve pool, functioned as an extra carbon pool for catabolic and metabolic purposes.

In addition to the uptake of orthophosphate, Phaeocystis is well capable of utilizing, after hydrolysis, various phosphomonoesters as a phosphate source. Culture experiments showed that the hydrolysis of a whole range of nucleotides by means of alkaline phosphatases, equals the uptake rate of inorganic phosphate (chapter 7). Similar observations were also found for field samples where the calculated rate of hydrolysis of natural phosphomonoesters was high and sometimes equal to the uptake of inorganic phosphate. Therefore, Phaeocystis is considered to be well capable at times of phosphate shortage to utilize not fully recycled

phosphate. Because the substrate, used for testing the phosphatase activity of the cells, has a relatively high molecular weight (525 MW) and can easily penetrate the colony, the exploitation of natural phosphomonoester by colonies is considered a realistic possibility.

During the spring bloom the succession of diatoms by Phaeocystis is accompanied by a decrease in nutrient availability. Parallel to this depletion a shift in the chemical composition of the phytoplankton is found (chapter 3). While in the early phase of the spring bloom, at that time dominated by diatoms, the protein production was considerable, implying a high growth rate, in the later phase of the spring bloom the production of small metabolites and carbohydrates increased, and consequently the chemically measured protein to carbohydrate ratio decreased. Also in this later phase the amount of newly fixed carbon excreted by the algae increased. Since both species composition and nutrient concentrations vary it is difficult to decide which of the two factors is responsible for the observed changes in the chemical composition of the phytoplankton.

The physiological properties of Phaeocystis in relation to the diversity and availability of various phosphate compounds were tested in a final survey during the spring of 1986 (chapter 8). It was shown that the nutrient status as well as the composition of various phosphate sources change considerably in the coastal zone of the North Sea, especially in the area encompassing the plume of the river Rhine. The observed high alkaline phosphatase activity, the high phosphate uptake rates and the short turnover rates of phosphate support the view that the phytoplankton populations (at that time dominated by Phaeocystis) in these areas are phosphorus limited.

It is concluded that the different capacities of single cells and colonies mentioned before enable Phaeocystis pouchetii to exploit a habitat where phosphate surplus and phosphate depletion are alternating.